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FIDELITY TO NESTING TERRITORY AMONG EUROPEAN SPARROWHAWKS IN THREE AREAS

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Abstract.—In three separate study areas, two in south Scotland and one in east-central England, about 70% of European Sparrowhawks (*Accipiter nisus*) trapped in successive years had stayed on the same nesting territory, while the remaining 30% had changed territories between one breeding season and the next. Comparing age-groups, the frequency of territory changes was greatest in 1–2 year birds and became progressively less in 2–3 year and older birds. The figures for the three age-groups were 53%, 29% and 24% in females, and 43%, 36% and 28% in males. Within each age group, birds were more likely to change territory after a nest failure than after a success. A change of territory was usually associated with a change of mate, and followed by an improvement in nest success. The same trends were evident, and the recorded frequencies were remarkably similar, in all three study areas. This was despite the fact that the three areas showed different population trends (one decreasing, another stable and a third increasing), and the most distant areas were separated by more than 350 km.

Fidelidad al territorio de anidar entre gavilanes de la especie *Accipiter nisus,* en tres áreas

Extracto.—En tres áreas de estudio separadas, dos en Escocia y una en la parte central este de Inglaterra, cerca del 70% de gavilanes *Accipiter nisus,* atrapados en años sucesivos, han permanecido en el mismo territorio de anidar; mientras que el 30% restante cambió de territorio entre un ciclo reproductivo y el siguiente. Comparando grupos por edad, la frecuencia en el cambio de territorio fue mayor en aves de 1–2 años, y se hizo progresivamente menor en aves de 2–3 ó más años. Las cifras para los tres grupos por edad fueron 53%, 29%, y 24% en hembras; y 43%, 36%, y 28% en machos. En cada grupo las aves fueron más suceptibles a cambiar de territorio después de un fallido intento de anidar que después de uno con éxito. Un cambio de territorio generalmente estuvo asociado con un cambio de pareja, y estuvo seguido por una mejora en el logro del nido. En las tres áreas de estudio las mismas tendencias fueron evidentes, así también las frecuencias registradas fueron remarcablemente similares. Esto fue así pese al hecho de que las tres áreas mostraron diferentes tendencias de población (una decreciente, otra estable, y la tercera en crecimiento), y las más distantes estaban separadas por más de 350 km.
[Traducción de Eudoxio Paredes-Ruiz]

Like many other birds of prey, European Sparrowhawks (*Accipiter nisus*) often breed in the same restricted localities year after year, creating traditional nesting territories used over long periods (Tinbergen 1946, Newton 1979). Because they feed on a wide range of small birds, sparrowhawks seldom experience marked year-to-year fluctuations in food supply, and in the absence of other major disturbances (see below), their breeding populations tend to remain fairly stable over long periods of years (Newton 1986). In this paper we examine fidelity to territory and mate among sparrowhawks nesting in two areas in south Scotland and in one area in east-central England. Emphasis is placed on the circumstances associated with territory changes and on the consequence of territory changes to both mate fidelity and subsequent nest success. For the two areas in south Scotland the findings largely substantiate those of an earlier analysis of smaller samples (Newton and Marquiss 1982); for the third area, in east-central England, the findings are presented here for the first time.

In all three areas European Sparrowhawks nested only in woodland, usually building a new nest each year near previous ones. Each year we caught many birds at their nests for banding and identification. We could then check which individuals had remained on the same nesting territories from one year to the next and which had changed territories. Because females were easier to capture than males, we gained much more information for females.

Study Areas

The populations in the three study areas showed different long-term trends. In Annandale, south Scotland (55°15′N 3°5′W), nest numbers in a 700 km^2 area declined during the 10-yr study from 110 in 1971 to 76 in 1980. This decline was associated with the felling of some well-grown woodland, and the consequent loss of prime nesting

and foraging habitat (Newton and Marquiss 1986). In Eskdale, also in south Scotland (55°16′N 3°25′W), nest numbers in a 200 km² area remained fairly stable, staying within 15% of the mean level of 34 during the 19-yr study (1972–90). This stability in population was associated with relative constancy in habitat. In Rockingham, east-central England (52°30′N 0°30′W), nest numbers in a 220 km² area increased during a 12-yr study from 3 in 1979 to 96 in 1990 (Wyllie and Newton 1991). This increase represented a recovery of the local population following its virtual elimination in the 1960s, probably by organochlorine pesticides (Newton and Wyllie 1992). It was not associated with a corresponding change in habitat availability. In all three study areas, nearest-neighbor distances between nesting territories in continuous woodland averaged 0.4–0.6 km, but elsewhere were often greater, depending largely on the distances between woods.

METHODS

In all three areas all suitable woodland was searched annually for nests, and attempts were made to catch as many breeders as possible. During nest-building, in April and early May, baited cage-traps were placed on the ground near nests, where possible next to regular perches or plucking sites. In this way both sexes could be caught. During incubation in late May and June, females were caught on their nests by use of noose carpets (for this operation, which took about 20 min, the eggs were replaced temporarily by dummy eggs to avoid breakages). As males do not incubate, only females could be caught in this way, but the method was effective only until hatch. In the late nestling and post-fledging stages, in July and early August, further attempts were made to catch breeders using cage-traps. Over the years, most of the females trapped were caught on the nests themselves. We had no evidence that either method of capture affected reproduction, for no differences in mean success were apparent between nests where birds were caught in cage traps, in noose carpets, or not caught at all (Newton 1986).

Sometimes in April we caught more than one male or more than one female near the same nest, making identification of the nest owners uncertain. We therefore stamped an individual number on the flight and tail feathers of all birds caught. As sparrowhawks began to molt after egg-laying, their shed feathers were often found near the nest, thus enabling us to check the identity of the incubating female against the one or more females caught earlier at the same site. Most females caught in April, before egg laying, were present on the same territory during incubation, but some were present on a different (usually neighboring) territory. Moreover, wherever more than one female was caught on the same territory in April, usually no more than one was present during incubation, and often the others were found incubating on other territories. From more than 2000 nest records, we had only seven instances (0.3%) of two females laying and incubating over the same period in the same nest (Newton 1986). The most likely interpretation of these findings is that sparrowhawks are usually monogamous, with one pair per nesting territory, and additional birds caught near nests were neighboring territory owners, non-breeders or other intruders. Because most of the females included in subsequent analyses were identified at a nest during incubation, we could be certain of their eventual affiliation. The same was not true for males, however, whose molted feathers were seldom found. This meant that we could not usually be certain that a male caught near a nest in April did eventually breed there, or when more than one male was caught, which (if any) was the owner.

Because more females than males were captured, fewer data were obtained for males, so records for males from the two Scottish areas were combined. Throughout this paper a nest in which young were raised to fledging is counted as successful, whereas one in which no young were raised is counted as failed, regardless of the stage of failure (in practice most failures occurred at the egg-stage; Newton 1986). In assessing the frequency of territory changes, birds which were forced to move through clear-cutting of their nesting areas were excluded.

RESULTS

Frequency of Territory Changes. The main findings were remarkably similar among areas, even though one was more than 350 km from the other two whose boundaries were only 15 km apart. Among females caught in successive years, 70–75% were on the same territory, while 25–30% had changed territories between years (Table 1). For females caught at intervals longer than one year, the figures for each area were consistent with an approximate 30% change between years (Table 1).

Dividing females into three age-groups, aged 1, 2 or 3+ yr respectively, revealed a progressive increase in site-fidelity between successive age-groups (Table 2). Overall around 53% of first year females changed territories for the next year, compared with 29% of second year females and 24% of older females. Moreover, within each age-group, changes of territory were significantly more frequent after a nest failure than after a success. Again the figures were remarkably similar among areas (Table 2).

The same trends were apparent in males, with (a) about 30% of birds changing territories between years (Table 1), (b) increasing site fidelity with advancing age (43%, 36% and 28% in successive age-groups), and (c) a greater tendency to change territories after a failure than after a success (Table 2). However, with smaller samples, these trends were seldom significant in particular age-groups or areas. In general, males that changed territories moved over shorter distances than did females (Table 3). Males almost invariably moved to adjacent territories, whereas many females moved to more distant territories, the record being 28 km from one study area to another. Nonetheless, the majority of moves by both sexes were less than 5 km.

Table 1. Frequency of territory changes (%) among sparrowhawks identified in more than one year. S = stayed on same territory, D = moved to different territory.

	Birds Retrapped After Minimal Intervals[a]							
	One Year		Two Years		Three Years		Four Years	
	S	D	S	D	S	D	S	D
Females								
Annandale	131 (70)	56 (30)	16	20	4	4	0	2
Eskdale	109 (75)	37 (25)	9	6	1	3	0	1
Rockingham	152 (70)	65 (30)	8	27	2	10	0	3
Males								
Annandale	22 (71)	9 (29)	5	2	2	0	0	1
Eskdale	4 (57)	3 (43)	0	1	1	0	0	0
Rockingham	43 (70)	18 (30)	4	10	2	4	0	3

[a] Different categories are mutually exclusive; percentages are included only for the largest samples of birds caught at one-year intervals

Consequences of Territory Changes. To determine the extent to which change of territory was associated with change of mate, analysis was necessarily restricted to those individuals whose mates were identified in successive years. In all three areas all four possible behavioral patterns were recorded, namely a bird was found in the second year (a) on the same territory with the same mate, (b) on the same territory with a different mate, (c) on a different territory with the same mate, or (d) on a different territory with a different mate. In some instances where a bird had a different mate, the original mate was known to be alive and breeding elsewhere, in other such instances the original mate was known to be dead, but most were of unknown status.

Pooling the overall data for both sexes, some 61% of birds that stayed on the same territory had retained the same mate, whereas only 28% of birds which changed territories retained the same mate (Table 4). All moves in which the pair stayed together were to an adjacent territory. It seems, therefore, that retention of the same territory was more often associated with retention of the same mate than was a change of territory.

As changes of territory were more frequent after a nesting failure than after a success, it was of interest to check whether birds bred more successfully after a move. We therefore examined nest-success before and after a move for all birds which changed territories; similar figures for birds which stayed on the same territories acted as the control. In all three areas, birds that stayed on the same territory had generally higher success than birds that moved, and often bred less successfully in the second year than in the first (significant in three of fifteen area-age combinations in Table 5). In contrast, birds that changed territory generally bred more successfully in the second year than in the first (significant in three of fifteen area-age combinations in Table 5). Again this tendency was apparent in both sexes. It thus seems that one advantage of a change in territory was an improved chance of nest success.

Discussion

The most striking finding was the consistency in behavior of European Sparrowhawks among areas. In all three areas, about the same proportion of individuals changed territories from year to year and similar relationships were apparent between territory fidelity, previous nest success and age. This consistency occurred, even though the three areas showed different population trends, and one area (Rockingham) was more than 350 km south of the others. Unlike some other raptors, such as the Marsh Hawk (*Circus cyaneus*; Hamerstrom 1969, 1986), the European Sparrowhawk is not noted for nomadism, and most of the movements recorded between territories were less than 5 km. In this respect, too, there was no obvious difference among areas. Probably in all areas the distances recorded were biased towards shorter values, because any birds which left the areas would usually not have been detected. However, the distances that most birds moved were small compared to the dimensions of the study areas.

Table 2. Frequency of territory changes by female sparrowhawks, according to area, age and previous nest success. S = stayed on same territory, D = moved to different territory. Data were from successive years only, the same individual may appear in more than one age comparison.

Area	Age-group	After Previous Nest Success		After Previous Nest Failure		Overall		Significance of Variation Between Successful and Failed Birds (P)
		S	D	S	D	S	D	
Females								
Annandale	1–2	6	3	2	10	8	13	0.03[a]
	2–3	17	3	1	3	18	6	0.04[a]
	3+	89	20	16	17	105	37	<0.001
	All birds (%)	112 (81)	26 (19)	19 (39)	30 (61)	131	56	<0.001
Significance of variation between age-groups		0.49		0.13		0.003		
Eskdale	1–2	4	5	1	4	5	9	0.58[a]
	2–3	17	4	3	8	20	12	0.01[a]
	3+	75	8	9	8	84	16	0.001
	All birds (%)	96 (85)	17 (15)	13 (39)	20 (61)	109	37	<0.001
Significance of variation between age-groups		0.001		0.25		<0.001		
Rockingham	1–2	22	10	2	9	24	19	0.01[a]
	2–3	31	5	3	7	34	12	0.001[a]
	3+	81	20	13	14	94	34	0.002
	All birds (%)	134 (79)	35 (21)	18 (38)	30 (62)	152	65	<0.001
Significance of variation between age-groups		0.20		0.19		0.08		
Males								
Annandale and Eskdale	1–2	2	1	1	0	3	1	1.00[a]
	2–3	4	0	0	3	4	7	0.03[a]
	3+	18	5	4	5	22	10	0.10[a]
	All birds (%)	24 (80)	6 (20)	5 (38)	8 (62)	29 (67)	14 (33)	0.01[a]
Significance of variation between age-groups		0.50		0.16		0.79		
Rockingham	1–2	6	3	4	6	10	9	0.37[a]
	2–3	10	0	2	2	12	2	0.07[a]
	3+	17	4	4	3	21	7	0.32[a]
	All birds (%)	33 (83)	7 (17)	10 (48)	11 (52)	43 (70)	18 (30)	0.01
Significance of variation between age-groups		0.16		0.78		0.09		

[a] F-probabilities calculated by Fisher's Exact Test (two-tailed), otherwise chi-square test was used with Yate's correction. Combined probabilities for all areas, calculated according to Sokal and Rohlf (1981:779–782) were as follows: 1) Behavior in relation to age: after previous success, females $\chi^2 = 18.5$, df = 6, $P < 0.01$, males $\chi^2 = 5.09$, df = 4, $P < 0.3$; after previous failure, females $\chi^2 = 10.17$, df = 6, $P < 0.2$, males $\chi^2 = 4.11$, df = 4, $P < 0.5$, overall, females $\chi^2 = 30.61$, df = 6, $P < 0.001$, males $\chi^2 = 5.22$, df = 4, $P < 0.3$. 2) Behavior in relation to previous nest fate: females aged 1–2 years $\chi^2 = 18.57$, df = 6, $P < 0.01$, females aged 2–3 years $\chi^2 = 30.75$, df = 6, $P < 0.001$, females aged 3+ years $\chi^2 = 40.06$, df = 6, $P < 0.001$, all females $\chi^2 = 41.45$, df = 6, $P < 0.001$; males aged 1–2 years $\chi^2 = 1.99$, df = 4, $P < 0.8$, males aged 2–3 years $\chi^2 = 12.52$, df = 4, $P < 0.02$, males aged 3+ years $\chi^2 = 6.98$, df = 4, $P < 0.20$, all males $\chi^2 = 19.28$, df = 4, $P < 0.001$.

Table 3. Distances moved by birds which changed nesting territories between successive years. The same individuals may appear in more than one comparison.

	Ages (Years)	Number of Moves of the Following Distances (km)				Geometric Mean Distance (km)
		<1.0	1.1–5.0	5.1–10.0	>10.0	
Females						
Annandale	1–2	2	8	2	1	2.5
	2–3	3	1	2	1	1.8
	3+	12	26	1	1	1.5[a]
Eskdale	1–2	1	7	1	0	2.2
	2–3	2	7	3	0	2.1
	3+	3	13	2	0	1.9
Rockingham	1–2	15	3	1	0	0.8
	2–3	3	8	0	1	2.9
	3+	24	7	2	1	1.8
Males						
Annandale and Eskdale	1–2	1	1	0	0	1.0
	2–3	2	2	0	0	1.0
	3+	9	4	0	0	0.7
Rockingham	1–2	3	2	2	1	1.9
	2–3	2	0	0	0	0.6
	3+	5	2	0	0	0.7

[a] Omits one outlier of 28 km.

In changing territories after nest failure, sparrowhawks may have been responding to failure as such. Alternatively, both the failure and the move may have occurred in response to some third factor, such as an unsatisfactory local food supply. This would fit with an earlier finding that sparrowhawks were more likely to leave territories with a poor history of occupancy and nest success than territories with a good history of occupancy and nest success (Newton and Marquiss 1982, Newton 1988). As radiotracking showed, the better the food supply the more sedentary sparrowhawks became, and the worse the food supply the more wide-ranging they became (Newton 1986). Radiotracking further showed that, outside the breeding season, the sexes acted largely independently of one another. It was therefore not surprising that, when individuals changed territories, they usually acquired different mates.

One obvious advantage of site-fidelity to the bird is familiarity with the area, which may enhance foraging success, predator avoidance, defense and other behavior which contributes to reproductive performance. Other things being equal, the longer a sparrowhawk has lived in a locality, the more it

Table 4. Fidelity to mate in relation to fidelity to territory. The figures refer to birds whose mates were identified in two successive years, but the same individuals may appear in more than one comparison.

	Annandale		Eskdale		Rockingham		Overall	
Behavior	Females	Males	Females	Males	Females	Males	Females	Males
On same territory with same mate	13	13	2	2	24	24	39	39
On same territory with different mate	9	14	2	3	12	9	23	26
On different territory with same mate	1	1	2	2	4	4	7	7
On different territory with different mate	6	11	0	1	10	8	16	20

Table 5. Relationship between site-fidelity and subsequent nest success, according to age and area.

	Breeding Attempts in											
	Annandale				Eskdale				Rockingham			
	Same Territory		Different Territories		Same Territory		Different Territories		Same Territory		Different Territories	
Age (Years)	Successful	Failed	Successful	Failed	Successful	Failed	Successful	Failed	Successful	Failed	Successful	Failed
Females[a]												
1	6	2	3	10	4	1	4	4	22	2	10	9
2	6	2	10	3	4	1	6	2	14	10	14	5
Significance of variation (P)	1.00[b]		0.02[b]		1.00[b]		0.61[b]		0.02		0.31	
2	16	1	3	3	17	2	4	8	31	3	5	7
3	16	1	3	3	17	2	8	4	29	5	8	4
Significance of variation (P)	1.00[b]		1.00[b]		1.00[b]		0.22[b]		0.71		0.41[b]	
≥3	84	18	21	17	73	10	7	9	81	13	20	14
≥4	71	31	20	18	67	16	14	2	70	24	23	11
Significance of variation (P)	0.05		1.00		0.29		0.03		0.07		0.62	
Overall, one year	106	21 (17)	27	30 (53)	94	13 (12)	15	21 (58)	134	18 (12)	35	30 (46)
Overall, next year	93	34 (27)	33	24 (42)	88	19 (18)	28	8 (22)	113	39 (26)	45	20 (31)
Significance of variation (P)	0.07		0.35		0.34		0.004		0.003		0.11	
Males[a]												
Overall, one year	16	4 (20)	5	6 (55)	3	1 (25)	4	2 (33)	33	7 (18)	7	14 (67)
Overall, next year	15	5 (25)	9	2 (18)	2	2 (50)	5	1 (17)	28	12 (30)	10	11 (52)
Significance of variation (P)	1.00[b]		0.18[b]		1.00[b]		1.00[b]		0.19		0.35	

[a] In each age comparison, the same individuals are represented at both ages.

[b] F-probabilities calculated by Fisher's Exact Test (two-tailed), otherwise chi-square test was used with Yate's correction.

has to lose by leaving it, which may be one reason for the declining tendency to change territories with increasing age. In addition, as a bird ages its social status may rise, increasing its ability to hold a high grade territory and reducing its chance of being displaced by another individual.

In an earlier analysis, based on smaller samples, males changed territories less often than females, but not significantly so (Newton and Marquiss 1982). In the present analysis, based on larger samples, no difference was evident. However, the number of apparent territory changes by males may have been exaggerated if some males were caught while hunting near a neighboring nest. As explained earlier, the affiliation of males to particular nests could not be checked as it could for females. Moreover, virtually all the apparent moves recorded for males were to neighboring territories, whereas many females moved over longer distances. At least in this respect, therefore, males showed greater 'site-fidelity' than females. A difference in site fidelity between the sexes has been noted in a wide range of other birds (Greenwood 1980), including other birds of prey (Newton 1979, Village 1990).

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